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### TWO NEW SPECIES OF THE LEPTODACTYLID FROG GENUS *PHRYNOPUS*, WITH COMMENTS ON THE PHYLOGENY OF THE GENUS

BY

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Within the tribe Eleutherodactylini of the Leptodactylidae there are several genera that are presumed to be derived from various groups of the mega-genus *Eleutherodactylus*. Among these is the Andean genus *Phrynopus*, which consists of fourteen species, five of which were named by Lynch (1975) in his review of the genus. Recent fieldwork in the Andes of northern and central Peru by field parties from the University of Kansas has yielded specimens of two new species, which are described below.

#### ACKNOWLEDGMENTS

For loan of specimens and/or provision of working space I am indebted to Marinus S. Hoogmoed, Robert F. Inger, and William E. Duellman. The latter and Thomas J. Berger were enjoyable field companions in Peru; fieldwork was supported by NSF grant DEB 76-09986 to William E. Duellman and by a NSF Graduate Fellowship to the author. Linda Ford and Darrel Frost critically read the manuscript. Laboratory facilities were made available by the Center for Biomedical Research of The University of Kansas. Permits for collecting were generously provided by Ing. Carlos Ponce del Prado, Dirección de Conservación, Lima, Peru.

#### MATERIALS AND METHODS

Statistical analyses were done using BMDP statistical software (Dixon, 1981). Cladograms were produced using the WAGNER78 program written by J. S. Farris. Drawings of the skulls were executed by means of a Wild M-8 microscope with camera lucida attachment. Skeletons were

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stained for cartilage and bone using the technique of Dingerkus and Uhler (1977). Photographs of preserved specimens were taken using a copy stand with the specimens completely immersed in water. The format of the diagnoses and measurements follows Lynch (1975). The following abbreviations for collections are used:

FMNH	Field Museum of Natural History
KU	The University of Kansas Museum of Natural History
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden

## SYSTEMATICS

### *Phrynopus nebulanastes*, new species

Fig. 1

*Holotype*.—KU 181407, an adult female from El Tambo, 31.5 km E Canchaque, 2770 m, Departamento Piura, Peru, collected 27 February 1979 by Thomas J. Berger, David C. Cannatella, and William E. Duellman.

*Paratypes*.—KU 181392, 181394-406 (26 Feb 1979) and KU 181408-414 (27 Feb 1979), same locality and collectors as the holotype.

*Referred specimens*.—KU 181415-16 (cleared and stained), same data as KU 181408-14; KU 181841 (young), same data as 181392.

*Diagnosis*.—A large *Phrynopus* (31.2-41.2 mm SVL, males and females combined); skin of dorsum and venter smooth; first finger longer than second; toes lacking basal webbing and lateral fringes; two metatarsal tubercles, inner slightly larger than outer; tarsus lacking tubercles or fold; tympanum present, reduced in size, concealed beneath skin; tympanic annulus, columella, and cavum tympanum present; snout sloping in lateral profile; males lacking vocal slits; prevomerine teeth present on prominent processes lying median and posterior to choanae; frontoparietals almost in median contact, lacking crests; nasal bones large, in median contact; anterior ramus of parasphenoid reaching level of, but not in contact with palatines; median ramus of pterygoid in slight contact with parasphenoid alae; dorsum brown, black, or dull green in life; venter greenish yellow with brown or gray mottling, ventral surfaces of hind limbs and spots on groin and thighs bright yellow.

The presence of prevomerine teeth and a tympanum concealed by skin distinguishes *P. nebulanastes* from other species except *P. parkeri* and *P. nanus*. The latter is easily distinguished from *P. nebulanastes*: *P. nanus* is a much smaller frog (21.3-24.5,  $\bar{x}$  = 23.1 mm, n = 9 females), lacks the bright yellow markings on the hind limbs and concealed surfaces, and the first finger is shorter than the second.

In *P. parkeri* the TIB/SVL ratio is 37.1-43.8 (48.6-57.2 in *nebulanastes*). The two sympatric species can be distinguished readily by this relative difference in limb length (Fig. 3). Vocal slits are absent in both species (contra Lynch, 1975); the frontoparietals are rugose in *parkeri*, but smooth in *nebulanastes*. The skull is ossified more fully in *parkeri* than in *nebulanastes*; compare Fig. 10 in Lynch (1975) with Fig. 4 in this paper.

Also, indistinct dorsolateral stripes are seen in most specimens of *P. parkeri*, but these are never present in *nebulanastes*.

*Description.*—(Measurements summarized in Table 1) head narrower than body; head slightly longer than wide, head width 90.5-97.9% of head length; head width 48.6-57.2% of SVL; snout subacuminate in dorsal view, sloping in lateral profile, canthus rostralis sharp, slightly concave; loreal region concave; lips not flared; nostrils lateral, slightly protuberant; snout short, eye-nostril distance 86.8-109.7% of eye length; interorbital region flat, cranial crests absent; upper eyelid width 66.7-93.1% of IOD; tympanic ring, columella, and cavum tympanum present; tympanum concealed by skin; eustachian tubes absent; supratympanic fold weakly developed; tongue large, oval, not notched posteriorly, posterior one-third free; choanae small, round, not hidden by palatal shelf of maxillae; prevomerine dentigerous processes present, slanted posteriorly, wider than long, each bearing 2-7 fang-like teeth; processes separated by width equal to width of a choana; males lacking vocal slits and vocal sacs.

Skin of dorsum and venter smooth; dorsal skin finely areolate in a few individuals. Skin tuberculate in post-tympanic region, forming a hint of dorsolateral folds anteriorly; ulnar tubercles and folds absent; palmar tubercle not bifid, about as large as thenar tubercle; subarticular tubercles low, round, simple; fingers not fringed; first finger longer than second. Shank 48.6-57.2% of SVL; tarsal and heel tubercles absent; two metatarsal tubercles, inner tubercle elliptical, slightly larger than outer tubercle; supernumerary plantar tubercles absent; subarticular tubercles round to slightly oval; toes lacking lateral fringes and basal webbing.

In preservative, *P. nebulanastes* is dark brown above; the face is uniformly brown except for pale gray markings on the upper lip, which vary from a few scattered blotches to irregular or incomplete stripe (most specimens have an indistinct dark suborbital bar); the margin of the upper lip is dark brown; in a few specimens there is a hint of a dark brown canthal stripe; dorsal surfaces of limbs are brown with a few irregular gray markings; the gray-brown flanks fade into a pale grayish venter; the lower lip is dark brown; at one extreme the throat and venter are brown with large pale gray blotches; at the other extreme the entire ventral surface is pale gray; in several specimens there is a narrow middorsal line, beginning indistinctly in the scapular region and extending posteriorly across the anal opening, ending on the midline of the ventral surface of the thighs; at a point slightly dorsal to the anal opening this line is intersected by a line traversing the posterior face of the thigh and widening at the knee to form an irregular broad cream stripe on the ventral surface of the shank; the stripe continues onto the ventral surface of the tarsus as a narrow line, passing onto the plantar surface of the foot, where it branches into a narrow cream line on each digit; the concealed surfaces of the groin, thigh, and shanks are dark brown with cream blotches. In some specimens there are diffuse cream spots in the axillary region.

In life, the dorsum is brown, black, or dull green, with or without the creamy yellow line; the throat and belly are greenish yellow with darker

brown or gray markings; the ventral surfaces of the hind limbs and spots on the hidden surfaces of groin and hind limbs are bright yellow. The iris is dull bronze.

Three very small specimens (KU 181841) are pale brown, with darker bars on the limbs; the thin middorsal stripe extends from the tip of the snout to the anal opening and is also present on the posterior thighs; a dark suborbital bar is present.

*Measurements of the holotype in mm.*—Snout-vent length (SVL) 35.2, tibia length (TIB) 20.1, foot length (FOOT) 21.8, head length (HLEN) 13.3, head width (HWID) 12.9, interorbital distance (IOD) 2.8, inter-

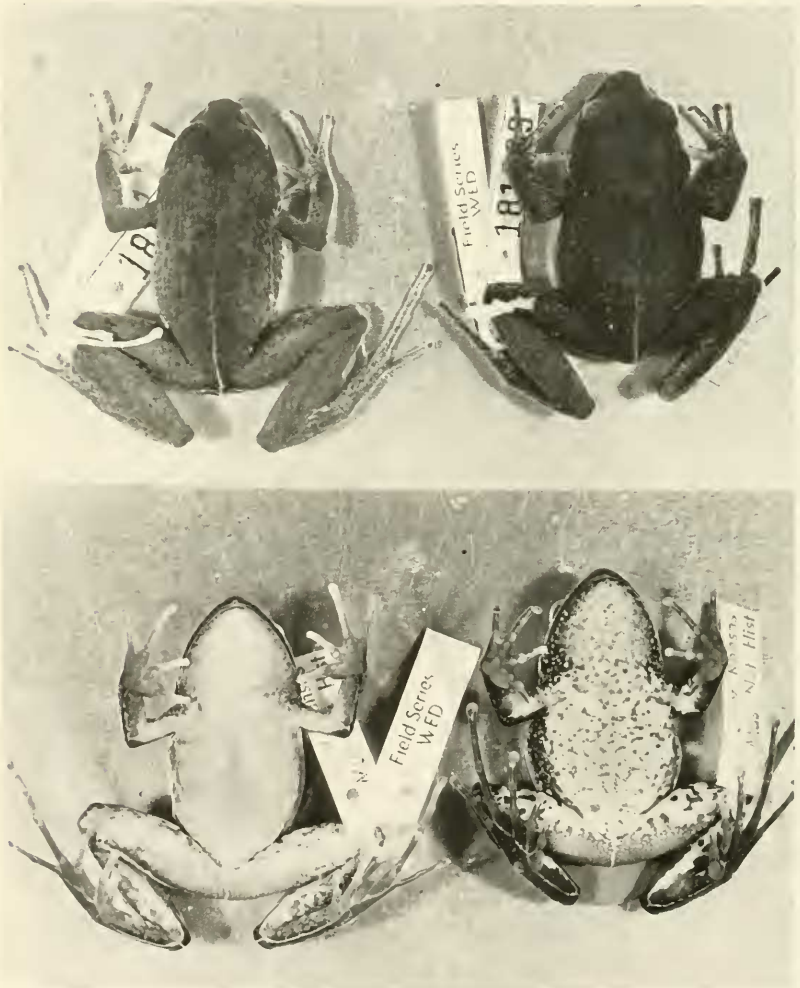


FIGURE 1.—Dorsal and ventral views of *Phrynopus nebulanastes*. Left: KU 181407, holotype, female. SVL = 35.2 mm. Right: KU 181399, paratype, male, SVL = 35.2 mm. Ventral patterns are indicative of variation seen in the species.

narial distance (IND) 3.5, eyelid width (ELID) 2.3, eye length (EYE) 3.8, distance from anterior corner of eye to nostril (ENOS) 3.3.

*Etymology*.—From Latin *nebula*, meaning fog, and Greek *nastes*, dweller, in reference to the elfin cloud forest where this species was found.

*Natural History*.—Individuals were found under rocks along the road in disturbed cloud forest. Some were calling at night; the call is a "tick-tick-tick." *Phrynopus parkeri* was collected syntopically.

*Distribution*.—Known only from the type-locality (Fig. 5).



FIGURE 2.—Dorsal and ventral views of *Phrynopus lucida*. Left: KU 162427, paratype, subadult male, SVL=21.8 mm. Right: KU 162435, holotype, female, SVL=35.7 mm. Smaller frog demonstrates the dorsolateral stripes seen in smaller specimens.

*Morphometrics.*—The measurement statistics are summarized in Table 1. Mann-Whitney U tests (between the sexes) were performed for each variable, and each test was significant ( $P < 0.05$ ) for all variables except IND, for which  $P = 0.08$ . Spearman's correlation coefficient was computed for SVL versus every other variable, and for EYE vs. ENOS, ELID vs. IOD, and HWID vs. HLEN, with the sexes treated as different groups. The correlation coefficients were significant only for SVL vs. TIB, SVL vs. FOOT, SVL vs. HWID, (males and females), SVL vs. IND, SVL vs. HLEN, and HWID vs. HLEN (males). In order to generate meaningful ratios of variables for descriptive purposes, the two variables must be significantly correlated. Because most of the correlations for pairs of variables within a sex were not significant, the data for males and females were pooled. The correlation coefficients for the pooled data were found to be highly significant for all of the tested pairs of variables. Ratios were computed for TIB/SVL, HWID/SVL, ELID/IOD, ENOS/EYE, and HWID/HLEN (Table 1).

*Phrynopus lucida*, new species

Fig. 2

*Holotype.*—KU 162435, an adult female from the north slope of Abra

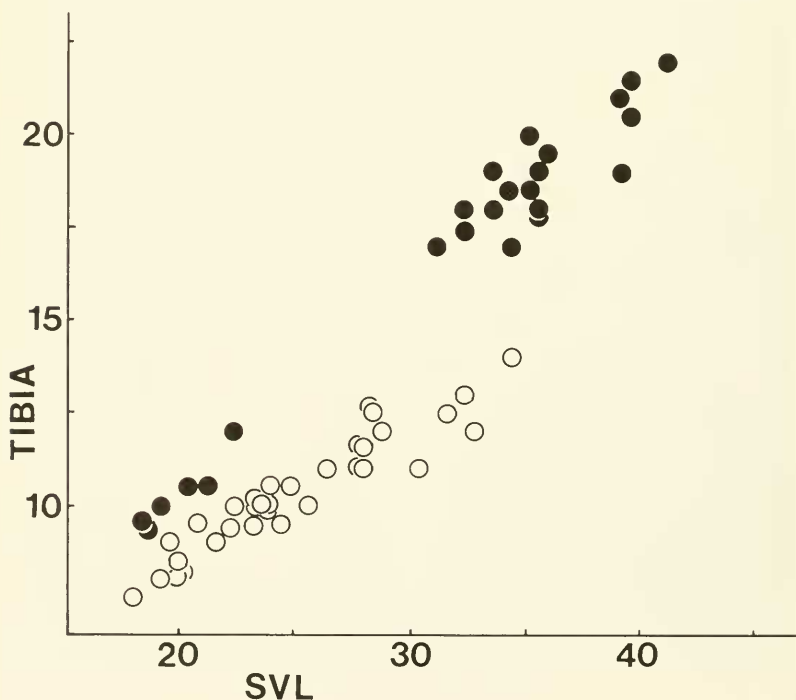


FIGURE 3.—Plot of tibia length vs. snout-vent length for adult and juvenile frogs of both sexes of *P. parkeri* (open circles) and *P. nebulanastes* (closed circles).

Tapuna, 7 km N Mahuayura, 3710 m, Departamento Ayacucho, Peru, collected 22 February 1975 by William E. Duellman and John E. Simmons.

*Paratypes*.—KU 162427-34 and 162436-38, FMNH 204170-204176, RMNH 17822 (WED 47190-91), same data as the holotype; KU 162439-45, Peru: Ayacucho: N slope Abra Tapuna, 10.5 km N Mahuayura, 3550 m, collected 19 February 1975 by William E. Duellman and Dana K. Duellman, and John E. Simmons; KU 162446-48, Peru: Ayacucho: 14 km SW Cano, 3250 m, collected 22 February 1975, by John E. Simmons; KU 162449-59, Peru: Ayacucho: 7.5 km SW Cano, 2970 m, collected 22 February 1975 by William E. Duellman and John E. Simmons.

*Referred specimens*.—KU 164065-67, collected by John E. Simmons, other data same as KU 162427-38, FMNH 39768-77, Peru: Ayacucho: La Mar, Yanamonte, 2400-2900 m, collected September 1941 by Felix Weyshowski.

*Diagnosis*.—A large *Phrynopus* (27.9-38.2 mm SVL, males and females combined); skin of dorsum smooth or barely areolate; skin of

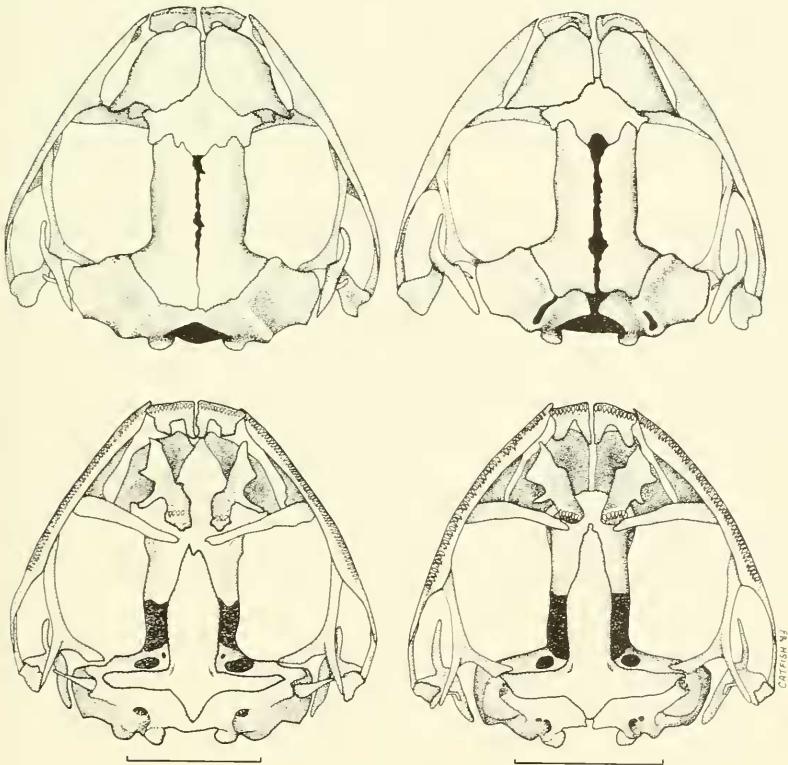


FIGURE 4.—Dorsal and ventral view of skulls of *P. lucida* (left, KU 164066, female) and *P. nebulanastes* (right, KU 181416, female). Scale equals 5 mm.

venter smooth; first finger slightly longer than second; toes lacking basal webbing and lateral fringes; two metatarsal tubercles, inner slightly larger than outer; tarsus lacking tubercles or fold; tympanum present, visible externally, its length 35.7-48.6% of eye length; tympanic annulus, columella, and cavum tympanum present; snout sloping in lateral profile; vocal slits present in most males (see Remarks); prevomerine teeth present on prominent processes lying median and posterior to choanae (Fig. 4); frontoparietals in broad median contact, lacking crests and rugosity; nasal bones large, in median contact; anterior ramus of parasphenoid reaching level of, but not in contact with, palatines; median ramus of pterygoid in slight contact with parasphenoid alae; dorsum dark gray to brown with brown or black markings, and in some individuals tan to orange dorsolateral stripes in life; venter gray to creamy white with gray flecks; groin and hidden surfaces dull orange to orange-red; iris crimson.

Five other species of *Phrynopus* have prevomerine teeth and externally visible tympana: *brunneus*, *flavomaculatus*, *peraccai*, *pereger*, and *peruanus*. *Phrynopus peruanus* differs from *lucida* in having the first finger shorter than the second; *P. flavomaculatus* has frontoparietal crests. *Phrynopus brunneus* and *peraccai* are smaller species (SVL < 30 mm) lacking the distinctive dorsal pattern of *lucida*. *Phrynopus pereger* also lacks the dorsal pattern, and has shorter shanks (TIB/SVL = 39.0-48.6 compared to 49.2-54.8 in *lucida*) and much more distinctive tubercles on the hands and feet. In addition, the dark brown ventral markings and cream middorsal stripe found in some individuals of *pereger* are not present in *lucida*.

*Description.*—(Measurements summarized in Table 1) head narrower than body; head slightly longer than wide; head width 88.7-96.4% of head length; head width 35.2-39.3% of SVL; snout subacuminate in dorsal view, sloping in lateral profile, canthus rostralis sharp, slightly concave; loreal region concave; lips not flared; nostrils lateral, slightly protuberant; snout short, eye-nostril distance 78.6-105.0% of eye length; interorbital region flat, cranial crests absent; upper eyelid width 63.6-80.6% of IOD; tympanum, columella, and cavum tympanum present; tympanum diameter 35.7-48.6% of eye length; eustachian tubes present; supratympanic fold prominent; tongue large, oval, not notched posteriorly, posterior one-third free; choanae small, oval, not hidden by palatal shelf of maxillae; prevomerine dentigerous processes present, slanted slightly posteriorly, wider than long, each bearing several normal teeth; processes separated by distance equal to width of a choana; vocal slits and sacs present in males.

Skin of dorsum smooth or slightly areolate; skin of venter smooth; large tubercle present immediately posterior to corner of mouth and inferior to supratympanic fold; hint of dorsolateral folds anteriorly; ulnar tubercles and folds absent; palmar tubercle bifid, slightly larger than thenar tubercle; subarticular tubercles low, round, simple; fingers not fringed; first finger slightly longer than second. Shank 49.2-54.8% of SVL; tarsal and heel tubercles absent; two metatarsal tubercles, inner tubercle elliptical, slightly larger than outer tubercle; supernumerary



plantar tubercles absent; subarticular tubercles round to slightly oval; toes lacking lateral fringes and basal webbing.

In preservative, *P. lucida* is gray-brown above, with black and pale gray mottled patches; the face has a distinct black canthal stripe and suborbital bar; a black interorbital bar is present, as well as a black supratympanic stripe; the dorsal surfaces are pale gray-brown with dark markings; a distinct W-shaped black mark is present in the scapular region, and a black patch is present in the sacral region; pale dorsolateral

TABLE 1. Measurements and proportions of *P. nebulanastes* and *P. lucida*. Statistics are given as mean  $\pm$  2 SE; range below in parentheses.

	<i>P. nebulanastes</i>		<i>P. lucida</i>	
	Males N = 10	Females N = 8	Males N = 8	Females N = 11
SVL	34.02 $\pm$ 1.04 (31.2-36.0)	37.86 $\pm$ 1.83 (33.4-41.2)	30.65 $\pm$ 1.10 (27.9-32.6)	34.93 $\pm$ 1.52 (30.8-38.2)
TIB	17.97 $\pm$ 0.46 (17.0-19.3)	20.28 $\pm$ 0.86 (18.8-22.1)	16.01 $\pm$ 0.44 (14.7-16.7)	18.13 $\pm$ 0.56 (16.7-19.4)
FOOT	19.67 $\pm$ 0.58 (18.4-21.3)	21.83 $\pm$ 1.07 (19.6-24.2)	17.06 $\pm$ 0.43 (16.1-18.0)	19.50 $\pm$ 0.89 (17.0-21.4)
HLEN	13.08 $\pm$ 0.36 (11.8-13.8)	14.03 $\pm$ 0.42 (13.3-15.1)	12.11 $\pm$ 0.64 (10.3-13.3)	13.45 $\pm$ 0.32 (12.5-14.3)
HWID	12.23 $\pm$ 0.40 (11.0-13.1)	13.4 $\pm$ 0.45 (12.4-14.5)	11.41 $\pm$ 0.52 (9.9-12.3)	12.65 $\pm$ 0.40 (11.5-13.5)
IOD	2.83 $\pm$ 0.10 (2.6-3.1)	3.03 $\pm$ 0.10 (2.8-3.3)	3.21 $\pm$ 0.15 (2.8-3.5)	3.47 $\pm$ 0.11 (3.2-3.8)
IND	3.49 $\pm$ 0.12 (3.2-3.8)	3.66 $\pm$ 0.10 (3.5-3.9)	3.20 $\pm$ 0.14 (2.8-3.4)	3.40 $\pm$ 0.15 (3.0-3.7)
ELID	2.17 $\pm$ 0.08 (1.9-2.3)	2.55 $\pm$ 0.11 (2.3-2.7)	2.29 $\pm$ 0.15 (1.9-2.6)	2.45 $\pm$ 0.13 (2.1-2.7)
EYE	3.46 $\pm$ 0.16 (3.1-3.9)	3.84 $\pm$ 0.14 (3.4-4.1)	3.66 $\pm$ 0.22 (3.3-4.2)	4.14 $\pm$ 0.15 (3.7-4.5)
ENOS	3.38 $\pm$ 0.11 (3.0-3.7)	3.55 $\pm$ 0.08 (3.3-3.7)	3.36 $\pm$ 0.17 (3.0-3.7)	3.75 $\pm$ 0.18 (3.3-4.2)
TYMP	-- --	-- --	1.55 $\pm$ 0.12 (1.1-1.9)	1.75 $\pm$ 0.10 (1.4-2.0)
TIB/SVL	0.532 $\pm$ 0.011 (0.486-0.572)		0.521 $\pm$ 0.006 (0.492-0.548)	
HWID/SVL	0.357 $\pm$ 0.004 (0.342-0.372)		0.367 $\pm$ 0.006 (0.352-0.393)	
ELID/IOD	0.802 $\pm$ 0.031 (0.667-0.931)		0.709 $\pm$ 0.023 (0.636-0.806)	
ENOS/EYE	0.957 $\pm$ 0.032 (0.868-1.097)		0.917 $\pm$ 0.034 (0.786-1.050)	
HWID/HLEN	0.944 $\pm$ 0.010 (0.905-0.979)		0.942 $\pm$ 0.010 (0.887-0.964)	
TYMP/EYE	-- --		0.432 $\pm$ 0.018 (0.357-0.486)	

stripes are present in some individuals smaller than 28 mm SVL. The pale gray flanks fade into a creamy venter, with pale brown flecks present in the gular and pectoral regions of some individuals; the ventral surfaces of thighs are cream; the ventral surfaces of hands and feet are dark brown. The hidden surfaces lack markings.

Colors in life: "Dorsum dark gray to brown with dark brown to black markings and in some individuals tan to orange dorsolateral stripes. Groin and hidden surfaces of limbs in males orange-red. Venter gray. Iris crimson." (WED field notes, 22 Feb 1975). "Dorsum brown with black markings and orange-tan dorsolateral stripes. Groin and hidden surfaces of hind limbs pale, dull orange. Venter creamy white with gray flecks. Iris crimson." (WED field notes, 19 Feb 1975).

*Measurements of the holotype in mm.*—SVL 35.7, TIB 18.3, FOOT 19.3, HLEN 13.7, HWID 12.6, IOD 3.7, IND 3.4, ELID 2.6, EYE 4.3, ENOS 3.6, Tympanum diameter (TYMP) 1.4.

*Etymology.*—The specific epithet *lucida* is an English noun meaning the brightest star of a constellation. This noun is derived from the Latin *lux*, meaning light. The epithet refers to the distinctiveness of this frog's color pattern compared to other members of the genus, and is a noun in apposition.

*Natural History.*—Individuals were collected by day, under rocks in wet paramo with puna grass, ferns, moss and lichens, and in upper humid montane forest under rocks near a stream.

*Distribution.*—Known from four localities in the Andean Cordillera Oriental west of the Río Apurimac in Depto. Ayacucho, between 2970 and 3710 m (Fig. 5).

*Remarks.*—*Phrynopus pereger* also is found on the slopes from Tambo to the Río Apurimac, but at lower elevations (2460–2650 m). The two species are easily distinguished: *Phrynopus pereger* is a smaller, stockier frog with relatively shorter limbs, hands and feet; it lacks the distinctive color pattern of *P. lucida* (See Diagnosis).

Vocal slits are present in six of the eight males examined. The two males without slits are relatively small—30.9 and 27.9 mm SVL, and may be immature.

*Morphometrics.*—The measurement statistics are summarized in Table 1. Mann-Whitney U tests (between the sexes) were performed for each variable, and each test was significant ( $P < 0.05$ ) for all variables except IND and ELID. Spearman's correlation coefficient was computed as for *P. nebulanastes*, with the addition of SVL vs. TYMP (sexes treated separately). The correlation coefficients were significant for 15 of the 28 pairs tested. The data were pooled by sexes, and the resulting correlation coefficients were all highly significant. With the addition of TYMP/EYE, the same ratios were computed as for *P. nebulanastes* (Table 1).

## DISCUSSION

Lynch (1975) divided the fourteen species of *Phrynopus* into four species groups: the *flavomaculatus* group (*brunneus*, *columbianus*, *fla-*

*vomaculatus*, *parkeri*, *peraccai*, and *pereger*); *peruvianus* group (1 species); *simonsii* group (*simonsii* and *nanus*); *peruanus* group (*cophites*, *laplacai*, *montium*, *peruanus*, and *wettsteini*). He then employed the method of Camin and Sokal (1965) to produce a cladogram of relationships (Fig. 6A) and found that this analysis agreed rather well with his more subjective groupings. Lynch did not have data for *columbianus*, *nanus*, and *peruanus*.

Both of the species described here possess almost all of the features of Lynch's *flavomaculatus* group, and none of the features that diagnose the other groups. The diagnostic features of the *flavomaculatus* group are: first finger longer than second; skin smooth; toes lacking lateral fringes and basal webbing; tarsal tubercle absent; prevomerine teeth present on processes lying posteromedial to choanae; median pterygoid ramus in

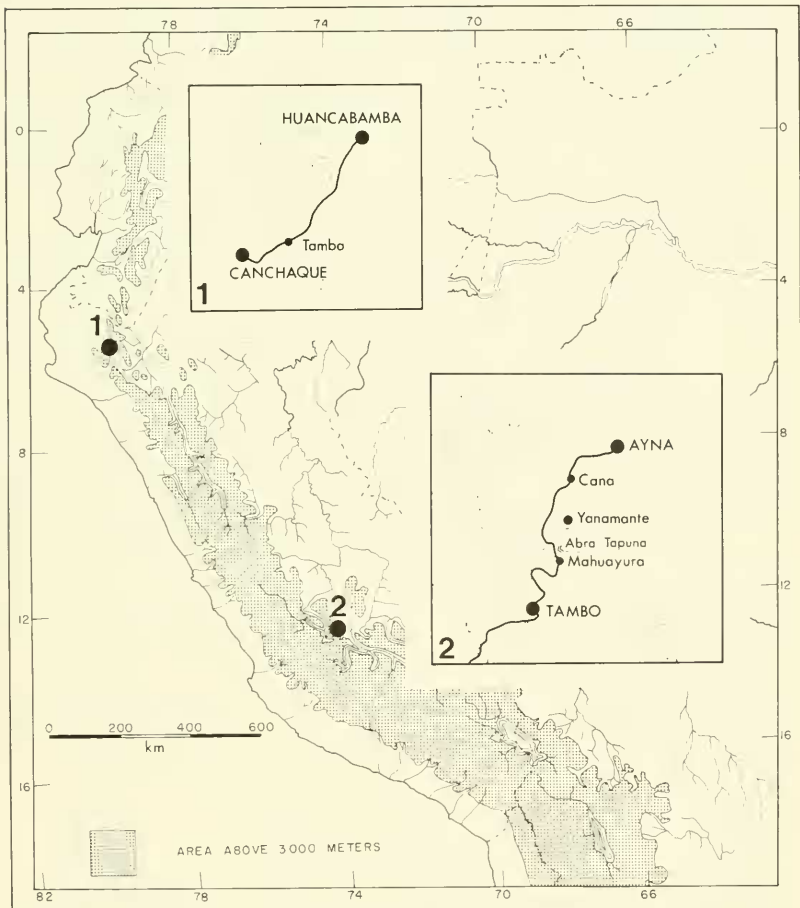


FIGURE 5.—Map of Peru showing type localities of *P. nebulanastes* (inset 1) and *P. lucida* (inset 2). Stippled lines on inset maps represent 3000 m contours.

contact with parasphenoid alae; anterior parasphenoid ramus in contact (or nearly so) with palatines; ears fully developed; pectoral girdle functionally arciferal; nasal bones large.

*Phrynopus nebulanastes* agrees with the above diagnosis except that the tympanum is reduced and concealed beneath the skin; the columella is also reduced (Fig. 4). *Phrynopus lucida* shares all of the features of the *flavomaculatus* group.

In order to assess relationships of the two new species, I have gathered the appropriate data to permit a reanalysis of the character-state data presented by Lynch (1975). Lynch (1975) did not include a data matrix, but as this information can be gleaned from his preferred cladogram, I have presented a matrix that includes data for the two new species (Table 2). The character-state tree for these characters is:

$$-1 \rightarrow 0 \rightarrow 1 \rightarrow 2 \rightarrow 3$$

To facilitate comparisons, I have included Lynch's description of character-states:

- 1.—Prevomers. 0: prevomer large, toothed; 1: prevomer large, toothless; 2: prevomer moderate-sized, edentate or not, denticulous ramus thin (sliver-like); 3: prevomer minute, denticulous ramus lost.
- 2.—Ears. 0: ear present, visible or concealed; 1: ear absent.
- 3.—Frontoparietals. 0: no cranial crests, no fontanelle (complete frontoparietals); 1: no cranial crests, fontanelle present; -1: cranial crests present, no fontanelle.
- 4.—Parasphenoid ala. 0: ala in contact with median pterygoid ramus; 1: ala narrowly separated from median pterygoid ramus; 2: ala widely separated from median pterygoid ramus.
- 5.—Anterior parasphenoid ramus. 0: not reaching palatines; 1: in contact with palatines.

TABLE 2. Character-state matrix for species of *Phrynopus*. The taxon ANCESTOR represents the hypothetical outgroup that possesses the primitive states of all characters.

											Character		Taxon
1	2	3	4	5	6	7	8	9	10	11			
0	0	0	0	0	0	0	0	0	0	0	0	ANCESTOR	
0	0	0	0	1	0	0	0	1	0	0	0	<i>brunneus</i>	
2	1	1	2	0	1	1	1	1	0	1	1	<i>cophites</i>	
0	0	-1	0	1	0	0	0	1	1	1	1	<i>flavomaculatus</i>	
2	0	0	2	0	1	1	0	1	0	1	1	<i>laplacai</i>	
0	0	0	0	1	0	0	0	1	1	1	1	<i>lucida</i>	
2	0	0	1	0	1	1	1	1	0	0	0	<i>montium</i>	
0	0	0	0	1	0	0	0	1	1	1	1	<i>nebulanastes</i>	
0	0	0	0	1	0	0	0	1	1	1	1	<i>parkeri</i>	
0	0	0	1	0	1	0	0	1	0	1	1	<i>peraccai</i>	
0	0	0	0	1	0	0	0	1	0	1	1	<i>pereger</i>	
3	0	0	2	0	1	0	0	1	0	1	1	<i>peruvianus</i>	
1	1	0	0	1	1	1	1	0	0	0	0	<i>simonsii</i>	
2	0	0	2	0	1	1	1	1	0	0	0	<i>wettsteini</i>	

- 6.—Nasal bones. 0: large nasals, in broad median contact; 1: nasals smaller, narrowly to relatively widely separated medially.
- 7.—Skin of venter. 0: texture smooth; 1: texture coarsely areolate.
- 8.—Finger lengths (I and II). 0: thumb longer than second finger; 1: thumb not longer than second finger, usually shorter.
- 9.—Toe fringes. 0: present; 1: absent.
- 10.—Snout shape. 0: rounded or truncate in lateral profile; 1: sloping in lateral profile.
- 11.—Metatarsal tubercles. 0: outer metatarsal tubercle much smaller than inner; 1: outer metatarsal tubercle more than one-half size of inner (equal in most cases).

A reassessment of Lynch's polarities is beyond the scope of this paper; however, I did find two discrepancies between the data presented in the text and on the tree. For *P. peraccai* the condition of character 4 is given in the tree as state 1 but is described on page 30 as state 0. For *P. simonsii* the tree lists state 0 of character 11, whereas on page 9 the tubercles are described as "subequal in size" (state 1), but on page 39 as "inner twice as large as outer" (state 0). In both cases I have used the data as presented on the cladogram, which has been included here for ease of comparison (Fig. 6A).

The methodology employed by Lynch (1975) yielded a 27 step tree without reversals in any of the characters, but with many convergences. The consistency ratio, as defined by Farris (1969) is 0.56. Consistency ratios range from 0 to 1; a value of 1 indicates a perfect fit (no homoplasy) of data to the tree. The value approaches 0 as the amount of homoplasy increases.

Two analyses of the original data were performed using the WAGNER78 program. In the first, the branching pattern of Lynch's tree was specified using the OPT option. This procedure "forces" the characters onto Lynch's tree in order to determine whether there was a more economical solution to the evolution of the characters. The second analysis (discussed below) included the new data from the species *lucida* and *nebulanastes*.

The first analysis produced a shorter tree of 26 steps (Fig. 6B), for which the consistency ratio is 0.58. Some noteworthy differences between the two trees (Figs. 6A, 6B) are: 1) the *flavomaculatus* group is monophyletic in the original cladogram, but in the second there is an unresolved trichotomy. Character 9 (the synapomorphy of the group) arose twice in the first; in the second it arose and reversed to the primitive state. The solutions are equally parsimonious, but the second results in a nonmonophyletic (or unresolved) *flavomaculatus* group; 2) In the first tree *montium* and *wettsteini* are sister-species, but their relationship is unresolved in the second (Fig. 6B). However, an equally parsimonious solution for character 8 (as in the first tree) results in the two species forming a monophyletic group; 3) *laplacai* and *cophites* are sister-species in the first, but not the second cladogram. This is due to the more parsimonious solution for the evolution of character 7 (3 steps in the first tree but only 2

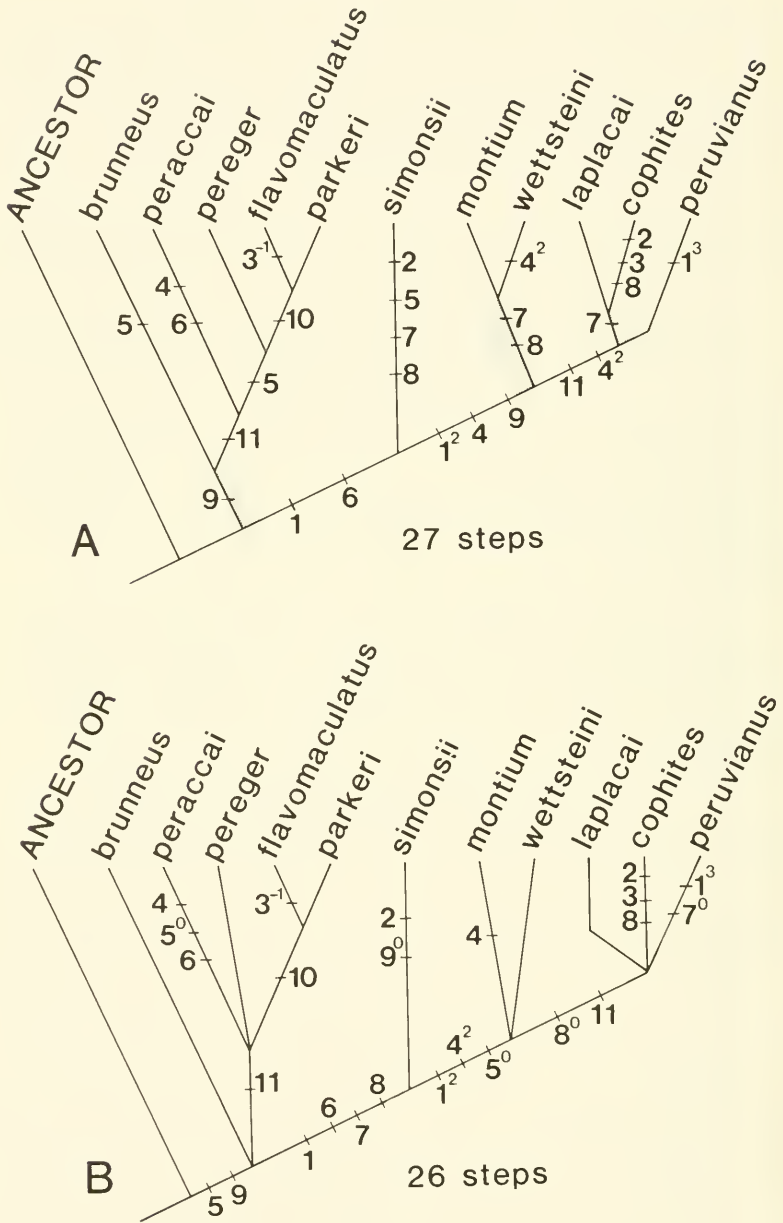


FIGURE 6.—A: original cladogram of Lynch (1975). B: Alternate cladogram produced by allowing reversals, yet preserving the original topology of the above. Three internodes (in gray) on the above tree have collapsed because no characters are present. The second tree has only 25 tie marks (instead of 26) because the evolution of character-state 4-2 in this tree implies 4-1 at the same internode.

in the second); 4) In the first tree character 5 arose three times, whereas in the second tree it arose once and reversed twice to the primitive state. The two solutions are equally parsimonious; however, the second treats character 5 (and also 9) as synapomorphies for the species of *Phrynopus*, whereas the first tree had no synapomorphies for the genus other than the structure of the digits, which was not included in the data matrix; 5) The two trees show different but equally parsimonious solutions for character 4. In the first, character state 4-2 arose twice; in the second it evolved only once, but reversed to 4-1 in *montium*. If one applies this first solution to the second tree, then *wettsteini* is more closely related to the *laplacai-cophites-peruvianus* cluster than to *montium*. This produces a tree topology at odds with the original, rather than the uninformative trichotomy as in the previous examples.

In summary, one can generate a tree that is shorter by one step by reinterpreting the evolution of character 7 (collapsing one internode), and equally parsimonious solutions for characters 4, 5, 8, and 9 can collapse two additional internodes, removing the monophyletic nature of some clusters.

In the second analysis, the original data were used to generate a cladogram in the usual fashion of allowing the program to compute the branching sequences. The order of the taxa was randomly shuffled 20 times, because the program may yield trees of slightly different lengths for data sets with much homoplasy. However, only a single tree (23 steps) was produced (Fig. 7), with a consistency ratio of 0.65. Because the data for *lucida* and *nebulanastes* are identical with those of *parkeri*, these taxa can

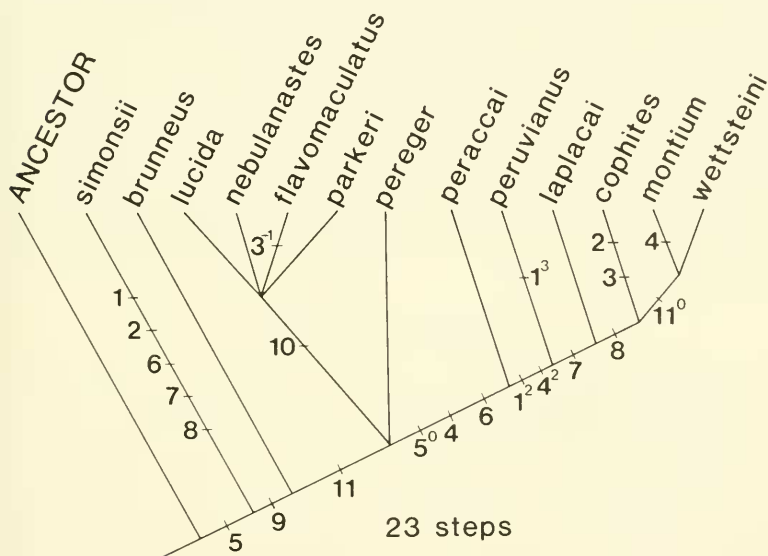


FIGURE 7.—Most parsimonious cladogram of the genus *Phrynopus*, using the data of Lynch (1975) and including the two new species described in this paper.

be added to the tree, and do not alter the shape or add to the number of steps. Features of the third tree are: 1) the *flavomaculatus* group is paraphyletic; 2) *P. simonsii* is the sister-species to all other *Phrynopus*; the fact that the five autapomorphies of *simonsii* are convergences with features of the *peruvianus-peruanus* group suggests that a careful reassessment of the data of *simonsii* is needed; 3) the *peruanus* group is monophyletic with *peruvianus* as its sister-group, whereas in the original tree the *peruanus* group was paraphyletic with respect to *peruvianus*; 4) the species *lucida* and *nebulanastes* cluster with *parkeri* because the data for these three species are identical; and 5) only characters 5 and 11 exhibit reversals in the third tree. The reversal of character 5 suggests that the polarity is incorrect. The derived states of the other bony characters (1, 2, 3, 4, 6) indicate a reduction in degree of ossification, whereas the derived state of character 5 suggests an increase. Reversing the polarity of character 5 brings it into accord with a more general pattern of reduction in ossification. A posteriori reversal of the polarity of character 5 reduces the length of the tree by one step.

Differences between the first two trees (Figs. 6A, 6B) are not substantial. I consider the third tree (Fig. 7) to be the best explanation of the data because it is the simplest. However, I defer from offering formal redefinitions of Lynch's groups for the following reason: In assessing the polarity of the characters Lynch considered that the character-states that were widespread among frogs in general to be primitive, as well as character-states occurring in primitive eleutherodactyline genera (*Hylactophryne* and *Ischnocnema*). The arguments against using widespread states as plesiomorphies are well-established in phylogenetic literature (Wiley, 1981). The primitive eleutherodactyline genera *Ischnocnema* and *Hylactophryne* are also not appropriate outgroups, if Lynch (1975:47) is correct in his assumption that *Phrynopus* is derived from an *Eleutherodactylus* stock "not unlike the group of species now represented by *E. cruralis*, *E. elassodiscus*, *E. granulosus*, and *E. nigrovittatus*." These species, then, may be inferred to be a more appropriate outgroup for assessing polarities, although Lynch does not provide synapomorphies that ally these species to *Phrynopus*. Hopefully, a phylogenetic analysis of these narrow-toed *Eleutherodactylus* will elucidate relationships within the genus *Phrynopus*.

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